OBSERVATIONS ON THE SAGITTARIA SUBULATA COMPLEX[1]

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The *Sagittaria subulata* complex has been variously interpreted by recent authors. Small (1933) recognized four species, *S. subulata* (L.) Buch., *S. stagnorum* Small, *S. lorata* (Chapm.) Small, and *S. filiformis* J. G. Smith. Seven years later Fernald (1940) interpreted the group as a single species, *S. subulata*, with four "fairly marked varieties," var. *natans* (Michx.) J. G. Smith, var. *gracillima* (Wats.) J. G. Smith, var. *lorata* (Chapm.) Fernald, and var. *typica*. The following year Clausen (1941) concurred with Fernald that *S. subulata*, *S. natans*, and *S. lorata* were conspecific. Clausen, however, considered Fernald's varieties *natans* and *lorata* to be phases of a single subspecies, ssp. *lorata* (Chapm.) Clausen. The variety *gracillima* was thought by Clausen to be a deep water phase of the tidal mud flat plant, then known as *S. subulata* ssp. *typica*. In a recent revision of the genus Bogin (1955) recognized a single species with three varieties. He noted that this species, *S. subulata*, is "exceedingly plastic" in its vegetative body. His varieties were proposed "only hesitantly" since they "are all similar florally, and merge into one another vegetatively without sharp demarcation in structure or distribution." Bogin's conception of var. *subulata* included Fernald's varieties *natans*, *lorata*, and *typica* as well as Small's *S. stagnorum* and part of Smith's *S. filiformis*. In his circumscription of a second taxon, var. *gracillima*, Bogin included a portion of Small's *S. lorata* and part of *S. filiformis* J. G. Smith. Bogin's third variety included only the Florida plants named as *S. kurziana* by Glück in 1927.

It is apparent from the foregoing brief resume that the *Sagittaria subulata* complex is not well understood if one may presume that about the same kind of sample was available to each of the investigators. Much of the variance in interpretation is undoubtedly due to the exceedingly great plasticity which these plants, as well as other species in the

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genus, show in their vegetative responses to different environments and/or environmental fluctuations.

The junior author commenced to observe the *Sagittaria subulata* complex in the field several years ago while conducting general collecting in the northern Florida region. During the summer of 1959 numerous observations were made by Dr. Norlan C. Henderson[2] and the senior author. Since that time the present authors have continued to study these plants and all of our collective experience includes a not inconsiderable amount of observation in nature where forms that appear to represent the extremes occur, and where certain differing kinds of habitat fluctuations were evident. In addition it includes some greenhouse culture experiments. It is our intent here to report upon this work only insofar as it leads us to offer some hypotheses as to the taxonomy of the complex and to suggest procedures for further intensive investigation to test these ideas.

Throughout most of these investigations the authors have entertained the notion that at least three biological entities were involved. One of these, the largest and most conspicuous, was thought to be referable to *Sagittaria kurziana* Glück. Plants of this type are very abundant in the St. Marks and Wakulla river channels (Wakulla County, south of Tallahassee, Florida) as well as in several of the large springs and spring-fed streams in central Florida. A second kind of *Sagittaria*, considerably smaller in size, was observed on the tidal mud flats and banks along the lower portions of these two rivers. This plant was considered to be the same as the *S. subulata* of the tidal flats around Chesapeake Bay and northward. A third aspect with floating dilated leaf blades was also recognizable and referred to Small's *S. stagnorum* (= *S. natans* Michx., not Pallas). However, recent observations of the complex, especially at the Wakulla-St. Marks stations, have demonstrated that this idea must be revised.

It will be helpful in the following discussion to consider first the kind and nature of the three principal phases ob-

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servable within the *Sagittaria subulata* complex. We think that an analysis of the morphology of the recognizable extremes and the habitats in which they grow will provide a framework around which our other observations can be organized.

THE SAGITTARIA KURZIANA PHASE

Plants of this type were first brought to the attention of botanists by Hugo Glück (1927) who had been guided to the type locality by Dr. Herman Kurz, then Professor of Botany at Florida State College for Women (now Florida State University) at Tallahassee. Glück and Kurz observed and collected the plant in the Wakulla and St. Marks rivers in 1926. The tremendous size of the phyllodes and scapes greatly impressed Glück who remarked enthusiastically that, to the best of his knowledge, it is the "largest *Sagittaria* of the whole world!" He noted phyllodes as long as 3.3 meters but the present authors have not encountered any longer than about 2.5 meters.[3]

The "*Sagittaria kurziana*" plants are characterized by the great length of their strap-like phyllodial leaves, several of which issue from a very short stem (Fig. 1). Each phyllode tends to be broadest above the middle, tapering gradually toward the apex, and is more or less flattened with the veins usually evident as several prominent ridges on the lower surface (Fig. 2). When viewed from underwater these leaves are seen to cover the spring or stream bottom, a scene which brings to mind Agnes Arber's vivid description of the deep water phase of *S. sagittifolia*, a European species. Mrs. Arber wrote (1920, p. 12) that "the ribbon-leaves of *Sagittaria* . . . have a singular beauty when seen forming, as it were, a meadow beneath the surface of the water, moving in the current in a way that recalls a field of wheat swayed by the wind." The inflorescence scapes of the "*S. kurziana*" type of plant also become very long, often reaching 15-25 dm.

This distinctive *Sagittaria* seems to be much at home in the clear running water of the Wakulla and St. Marks rivers (and a few of their small tributaries). It is very abundant

[3]The notation on *Griscom 21059a* (GH) that the leaves reach a length of fifty feet needs verification before being accepted.

in the Wakulla River all the way to its source at the large fresh-water Wakulla Spring. The plant also grows in great abundance in at least ten other comparable springs and spring-fed streams of northern and central Florida. These aquatic habitats are unique, having been produced by a combination of climatic and geological forces (Whitford, 1956). A tremendous volume of water issues forth from

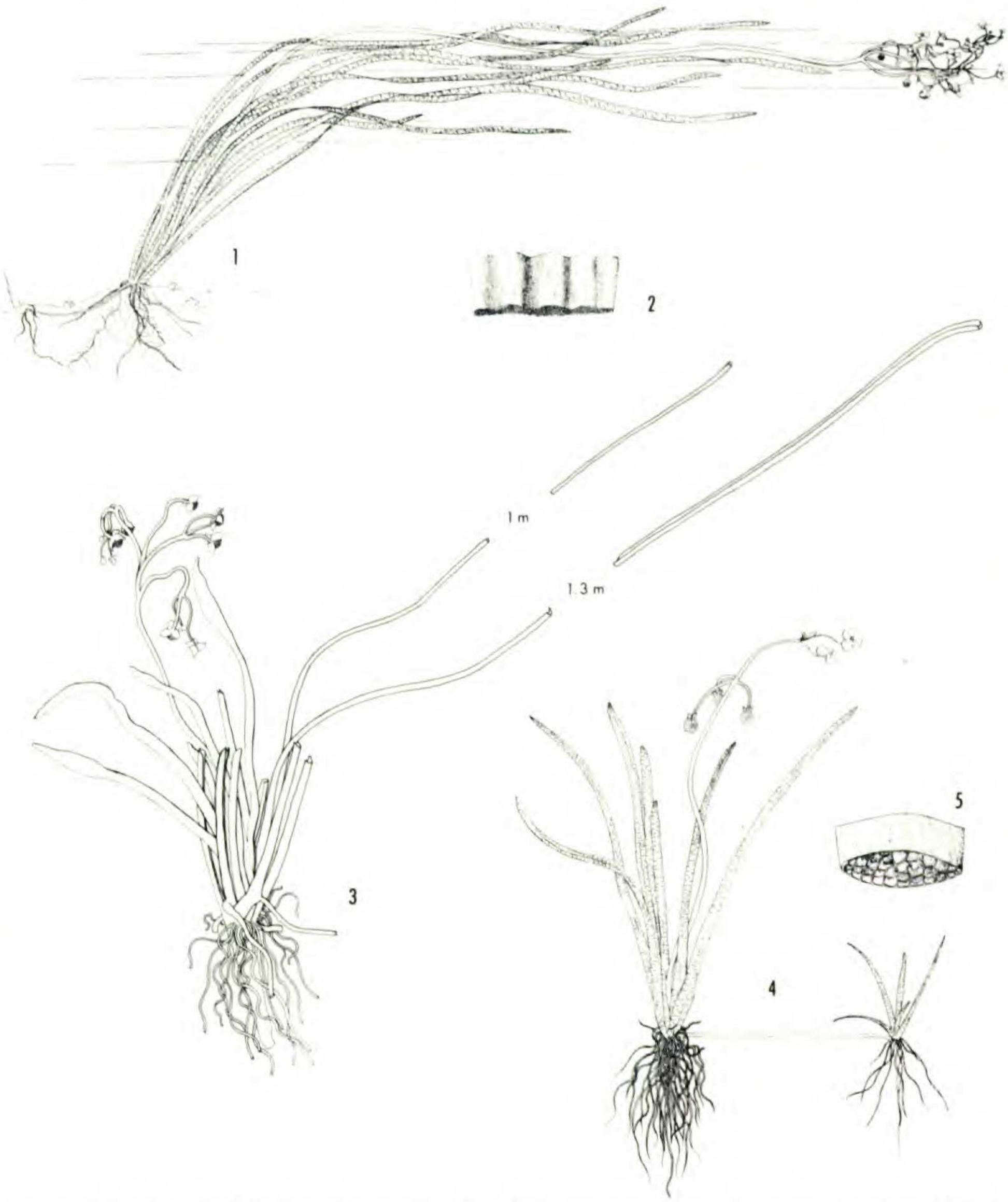

FIG. 1-5. FIG. 1. "*S. kurziana*," habit. Note young plantlet from rhizome. FIG. 2. Phyllode of "*S. kurziana*," cross-section, lower surface in face view. FIG. 3. "*S. kurziana*," plant uprooted and floating. Compare the much elongate original phyllodia with those formed while floating (see text). FIG. 4. "*S. subulata*," habit. Note young plantlet from rhizome. FIG. 5. Phyllode of "*S. subulata*," cross-section, lower surface in face view.

these giant springs, many having a flow of over three cubic meters per second. Around the springheads are often large open pools, and the water forms deep runs or streams which may be several miles long. Very little surface water enters and the chemical and thermal conditions are relatively stable, the light being the only important environmental variable (Whitford, 1956). The waters are hard in most of these springs, with large amounts of calcium, sodium, potassium and chlorides often present. The temperature is remarkably constant, varying less than 1° C. annually in many of the spring pools (slightly more down stream, of course). Wakulla Spring has a temperature of about 24° C. while several of those further south are a few degrees warmer.

In the St. Marks and Wakulla rivers the plants of the "*Sagittaria kurziana*" type grow in water from about one to at least three meters deep (completely submersed where the waters are affected by the tide) forming broad zones. In McBride's Slough, a spring and its stream that flows into the Wakulla River, the plants often grow throughout the width of the stream, especially near the springhead. Besides the *Sagittaria* other species of vascular plants are often present, including *Najas guadalupensis*, *Vallisneria* sp., and *Potamogeton illinoensis*. Dense beds of *Chara*, a large green alga, are also common. The leaves of these plants are coated with dense growths of algae, especially diatoms, filamentous greens, and blue-greens (Whitford, 1956). This investigator found that the algae form recognizable communities, well-developed on the *Sagittaria l*eaves, depending upon the mineral content of the springs.

The importance of these large springs and spring-fed streams in Florida as natural laboratories ready-made for ecological studies under controlled conditions has been shown by Odum (1957). From intensive investigations of community metabolism and productivity in one such spring, the famous Silver Springs near Ocala, Marion County, Florida, Odum found that a remarkable steady state is present and appears to have existed for a very long time. Under these optimum conditions Odum discovered that the *Sagittaria* plants are responsible for one-third of the primary produc-

tion of organic matter in the spring community. The *Sagittaria* no doubt plays a similar important role in the ecology of the other springs where it occurs.

THE SAGITTARIA SUBULATA PHASE

This distinctive *Sagittaria* of tidal mud flats and tidal shores was first collected by John Clayton sometime during the early seventeenth century. Clayton lived for many years in Gloucester County, Virginia (Stearn, 1957). While he visited and collected in other parts of Virginia, Clayton could have gotten his specimens of "*S. subulata*" near his home, since Gloucester County is bounded on the east by Chesapeake Bay and on the west by the York River.

The "*S. subulata*" phase is a small plant, commonly with short phyllodia (Fig. 4) not unlike those of *Lilaeopsis chinenses* (with which we have known it to be intermixed) and which by means of subterranean runners forms dense mats. In size, the shoots grade from the tiny *Lilaeopsis*-like ones on the upper tidal shores to a condition where there are rosettes of ascending wider leaves reaching a length of 1.5-3 dm. or more on lower shores (Fig. 10 a-i), submersed even at mean low tide. "Grassy" mats are formed on the bottom which very much resemble those formed by *Thalassia* in purely saline situations. The phyllodia tend to be more or less lenticular in cross-section, especially in the lower half, and, when fresh, as much as two-thirds to three-fourths as thick as they are wide (Fig. 5). Generally the veins are inconspicuous, not forming the prominent ridges as in the "*S. kurziana*" form. A tendency for the phyllodia to be broadened near their apices, producing a narrow but definite blade, is often present in plants of "*S. subulata*" from New York to North Carolina (Figs. 7, 8, 9).

The best development of the "*Sagittaria subulata*" form occurs on the tidal flats and along river shores which come under the influence of the tides. A few plants have been seen growing completely out of the water but they are probably covered during times of particularly high tide. For several hours each day (during the retreat and advance of the tide) most of the plants are exposed to the drying action of the sun and the air with little, if any, adverse

effects. Near the junction of the Wakulla and St. Marks rivers the "*S. subulata*" form is very abundant on the mud flats, often being virtually the only plant in a zone as wide as 30 meters. Seaward from this point even wider expanses of

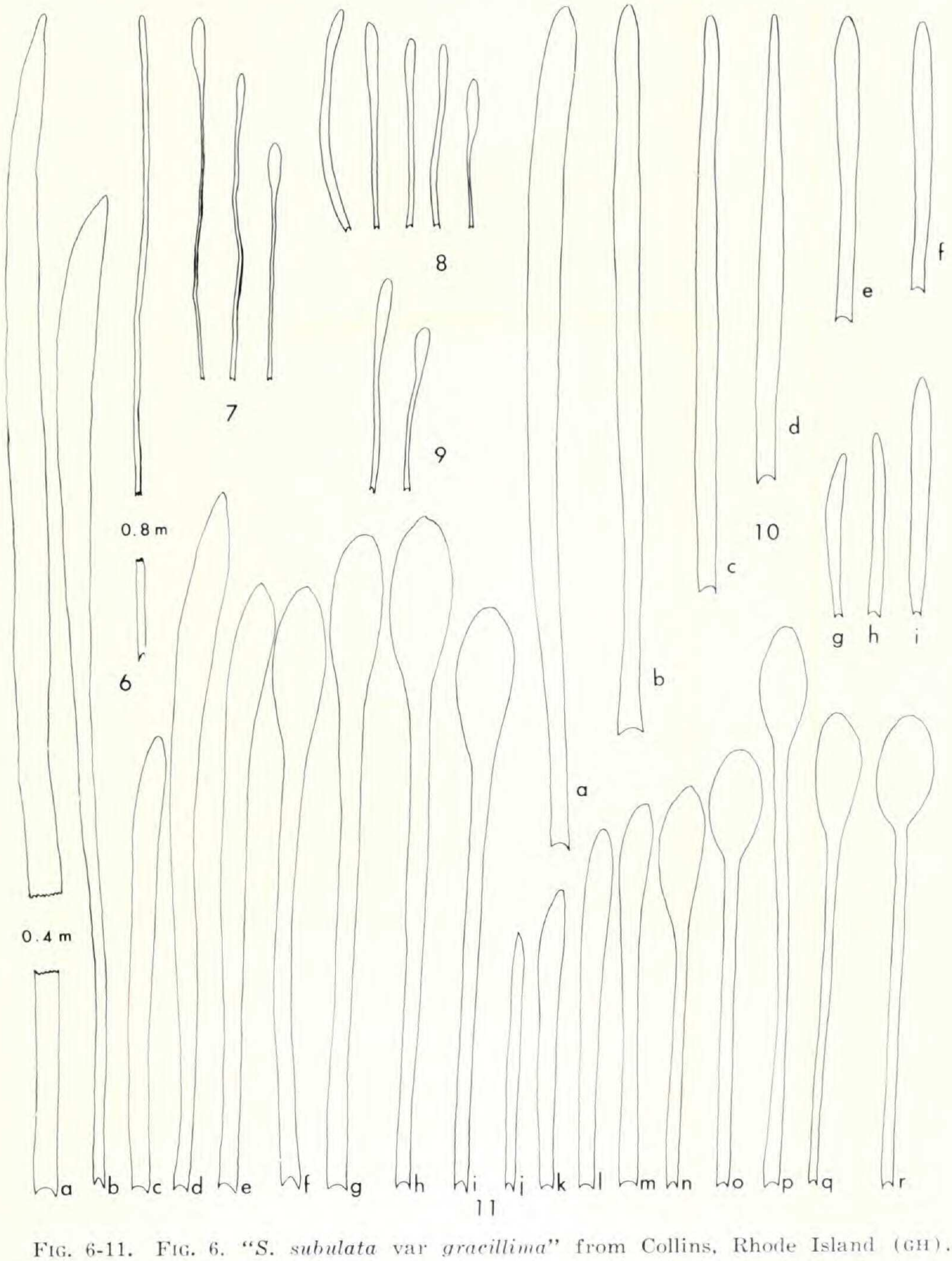

FIG. 6-11. FIG. 6. "*S. subulata* var *gracillima*" from Collins, Rhode Island (GH). FIG. 7. "*S. subulata*" from House 25070, Ulster Co., N. Y. (GH). Note widened lamina. FIG. 8. "*S. subulata*" from Steele Aug. 28, 1896, District of Columbia (US). FIG. 9. "*S. subulata*" from Steele Sept. 1, 1900, District of Columbia (US). FIG. 10 a-i. "*S. subulata*" from *Adams 728A*, Wakulla Co., Fla. (FSU). FIG. 11 a-r. "*S. kurziana*," population G, Wakulla Co., Fla. (See text).

the tidal flats are thickly carpeted with this plant. Upstream, further away from the tidal influence, the colonies diminish in extent, until only a few scattered individuals are present, as in the case at the U. S. Rt. 98 highway bridge over the Wakulla River (about seven miles from the Gulf of Mexico).

THE SAGITTARIA STAGNORUM PHASE

Plants of this taxon were first described by the elder Michaux in his "Flora Boreali-Americana" (1803) under the name of *S. natans* (an epithet unfortunately predated by *S. natans* Pallas, a European plant). Typically, many of the phyllodia are dilated near the apex, producing linear-ovate to ovate or even slightly sagittate blades which float upon the surface of the water (Figs. 12, 13). During the winter, the floating leaves disappear, presumably being killed by a thin film of ice which occasionally forms in this region. This medium-sized, very distinctive plant reaches its most typical development in the quiet, relatively shallow waters of sinkhole ponds and pools, lake margins, and swamps and roadside ditches in which water stands for several months. In the small sinkhole ponds which are a characteristic feature of the landscape in northern Florida the "*S. stagnorum*" phase often forms a zone or ring of considerable width around the margins. When the plants are in flower an unusual aspect suggesting confetti on the water surface is presented.

Additional Field and Greenhouse Observations

Having described in a general way the three main phases detectable within the *Sagittaria subulata* complex, we now turn our attention to the variations from these principal forms. Lest we be accused of so-called "typological thinking" may we hasten to assure the reader that this manner of organizing our observations is purely arbitrary. Due to the unusual nature of the problem this particular manner of presentation appears to us to be the best method. We are fully cognizant of the elementary biological principle that populations, subspecies, species — taxa if you please — vary in differing degrees. If the reader so wishes, he may regard each "phase" as representing the midpoint on a variation

curve; in a sense they can be called by the old-fashioned word "extremes."

Population[3] *A:* Marion Co., Fla., near Silver Springs, east of Ocala.

In a small drainage ditch which flows into an artificial boat basin near the Silver River (the stream from Silver Springs) *Sagittaria* plants with a most variable array of phyllodial shapes occur (*Henderson and Adams 2016* July 8, 1959, FSU, 8 sheets). All intermediate forms from strap-like phyllodia to leaves with fairly definite petioles and blades were observed, even on the same plant. The dilated leaf tips extended nearly vertically above the water surface with little or no tendency to become floating. Amidst the *Sagittaria* were numerous other kinds of vascular plants, resulting in the ditch being fairly choked with vegetation. The water depth in the middle of the ditch was about 70 cm. On the other side of a small footbridge, at the junction of the drainage ditch and the boat basin, were many *Sagittaria* plants with only long, strap-shaped phyllodia. Here the water was much deeper, the current fairly swift, and very few other plants were present. Since the *Sagittaria* in the nearby Silver River and Silver Springs had the "*S. kurziana*" appearance, this population was interpreted as being a deviation from the typical form of "*S. kurziana.*" More recently, study of similar populations in other areas has strongly suggested that a re-interpretation is necessary (see below).

Population B. Taylor Co., Fla.

A colony similar in several features to population A was discovered growing in a "black" water, swift-flowing stream out of a *Nyssa* swamp (8 miles south of Perry, *Godfrey and Houk 60460,* Oct. 21, 1960, FSU, 13 sheets). Many of the phyllodia were elongate and ribbonlike but all transitions to leaves with broadly dilated blades (Fig. 14 g-p) were present, even on the same individuals. The leaves on several

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[3]The presence of extensive vegetative reproduction by means of rhizomes and corms renders the collection of true population samples most difficult. Therefore, we have had to be satisfied with taking specimens along transits or by merely walking (or rather wading) about over the stand and picking up plants at irregular intervals (see fuller discussion of this phenomenon below).

plants were cut off about 8-12 cm. above the base and the rootstocks were planted in wet soil contained in aquaria. The tanks were filled with 12-15 cm. of tap water. Within a few days after transplanting, new leaves were being produced (*Godfrey 60460A*, March 1961, FSU, 8 sheets). These, as well as subsequent ones, tended to have a widened floating blade with slender "petiole" (Fig. 14 a-f). Such plants have the typical vegetative form characteristic of "*S. stagnorum*".

FIG. 12-13. "*Sagittaria stagnorum*," habit. Note the sagittate leaves.

Population C: Levy Co., Fla.

A population comparable to the Taylor County area (see B above) was found growing amidst a thick mat of the aquatic grass *Hydrochloa caroliniensis* in a drainage ditch bordering a cypress swamp (ca. 5.5 miles west of Bronson, *Godfrey 60559*, March 2, 1961, FSU, 4 sheets). In nature, these plants possessed phyllodia which exhibited much the same gamut of variations in shape as the Taylor County population except that the "petiole" of the leaves with blades were very much shorter and stouter. Within less than two weeks after being transferred to aquaria in the greenhouse, broad, floating leaf blades on narrow petiolar structures were being produced in abundance (the original leaves were not removed in this sample; they soon rotted away in the aquaria). In this example, also, the aquarium grown plants assumed the aspect typical of the "*S. stagnorum*" phase (*Godfrey 60559A*, April 17, 1961, FSU, 3 sheets).

Population D: Leon Co., Fla.

For more than a year the senior author has continually observed a colony of *Sagittaria* growing in the "black" water of a *Nyssa-Taxodium* swamp. During a period of heavy rains and consequent high water level the plants were in about 0.5 to 1.2 meters deep. Many of the phyllodia were elongate and strap-like but, especially in the shallower water, various forms of widened leaf tips were produced (15 miles north of Tallahassee, *Adams 431*, April 19, 1960, FSU, 12

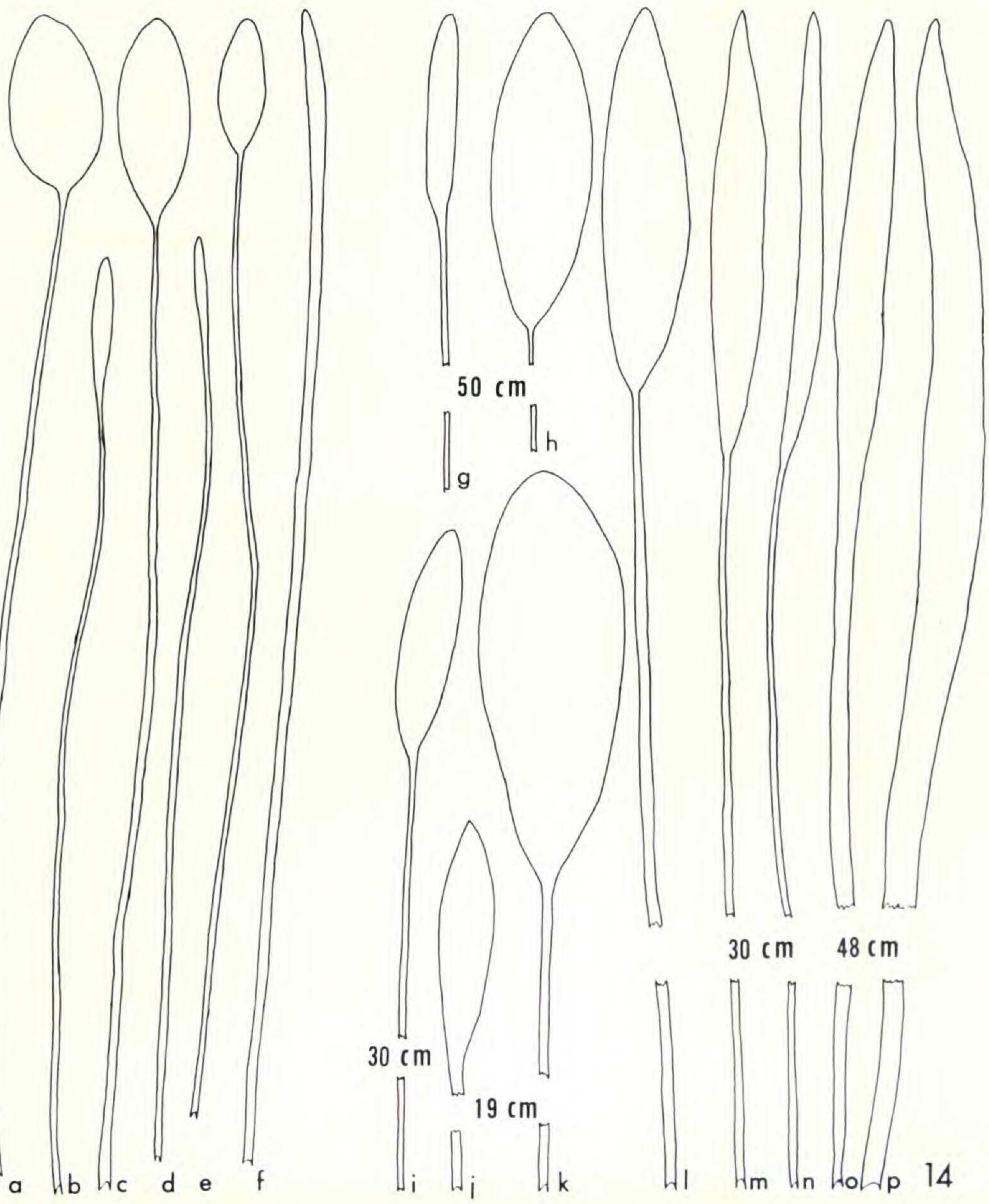


FIG. 14. "*S. stagnorum*," phyllodia: population B, Taylor Co., Fla.; a-f, plants grown in aquaria; g-p, plants in nature. (See text).

sheets). About five weeks later, the water level had dropped considerably and the plants presented a much changed appearance (*Adams 474*, May 21, 1960, FSU, 33 sheets). In the mud along the swamp margin were plants completely exposed to the air. Their leaves were very short, semi-erect, and with wide blades. Underground runners from these terrestial plants were traced out into the swamp bottom for distances of one-half to a meter or more. At intervals in the water new shoots were produced from these runners. The phyllodia were elongate and ribbon-like as well as with dilated, floating tips. Several rootstocks of the submerged individuals were transferred to aquaria and, within two weeks, most of the new leaves were of the floating type (*Adams 752*, March 30, 1961, FSU, 3 sheets).

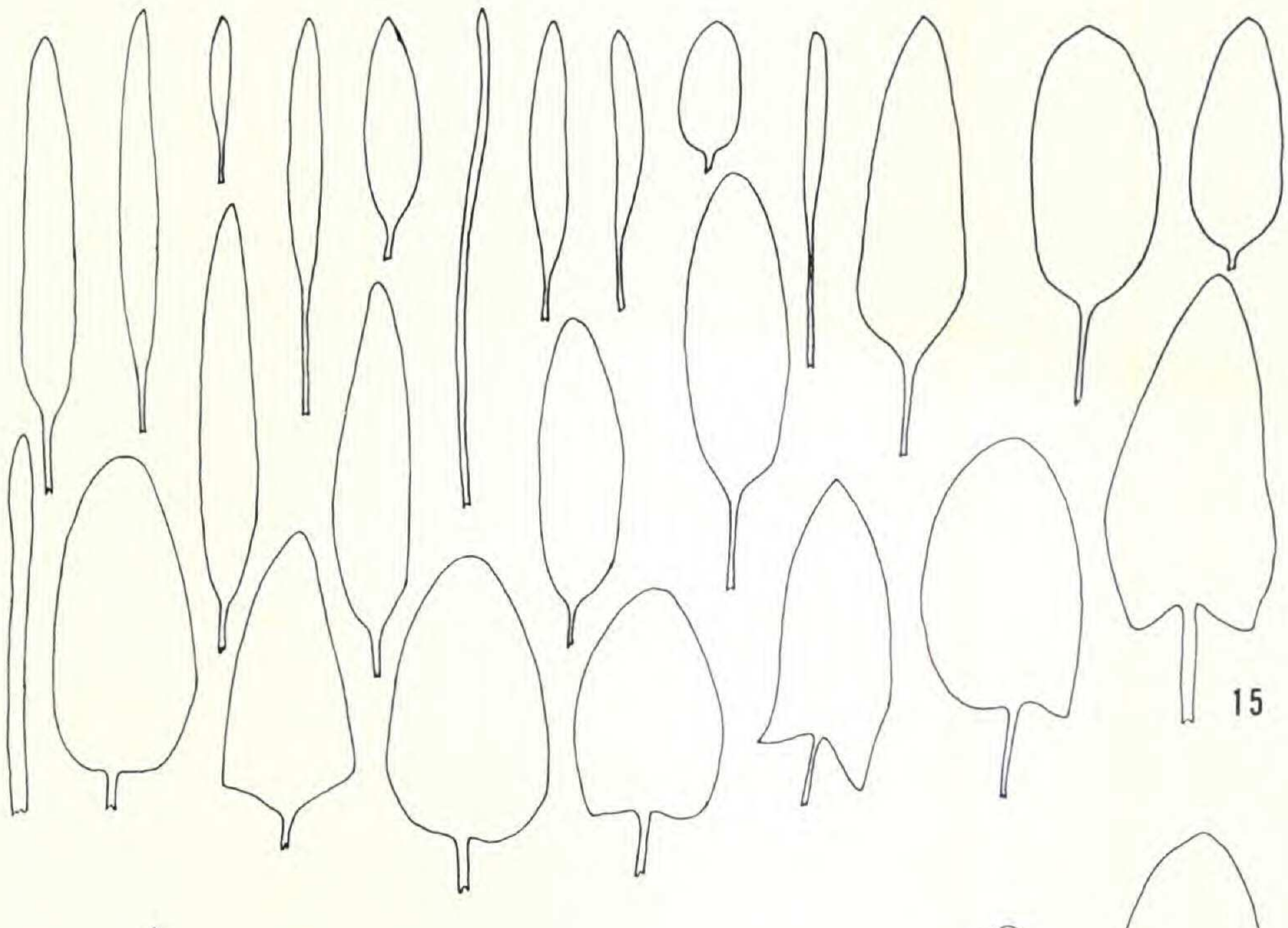
Population E: Leon Co., Fla.

Tremendous variation in the shape of the floating leaf blades is present in many populations referable to the "*Sagittaria stagnorum*" phase. The plants of one such colony in and on the exposed shores of a small pond had leaves showing all imaginable transitions from the ribbon-like phyllode to one with a dilated floating blade having a truncate or even somewhat sagittate base (Fig. 15) (1 mile north of Woodville, *Henderson 2003*, June 18, 1959, FSU, 5 sheets). A collection from the same pond (*Godfrey 57484*, Aug. 15, 1958, FSU, 27 sheets) made the previous summer is revealing since much more variability in leaf blade shape and size is present (Fig. 16). In general, the widened lamina were longer than in the Henderson collection while their bases tended to be more sagittate. Such annual changes in a population are of great interest and need to be investigated further. The tendency for production of sagittate leaves is evidently a widespread phenomenon, judging from the available herbarium material.

Population F: Wakulla Co., Fla.

Valuable information concerning the apparent effects of the local environmental conditions upon the vegetative bodies of the "*Sagittaria stagnorum*" form has been obtained by transect studies. One colony growing in a wide ditch adjacent to a *Nyssa* swamp was sampled by collecting the plants

at intervals along a transect reaching from the muddy bank out into the ever-deepening water (6 miles south of Crawfordville, *Adams 263*, Aug. 15, 1959, FSU, 8 sheets). Plants on the wet soil were dwarfed, their phyllodia rather short and with semi-erect dilated tips (Fig. 17a). Further out in the water (about 5-10 cm. depth) the typical floating blades



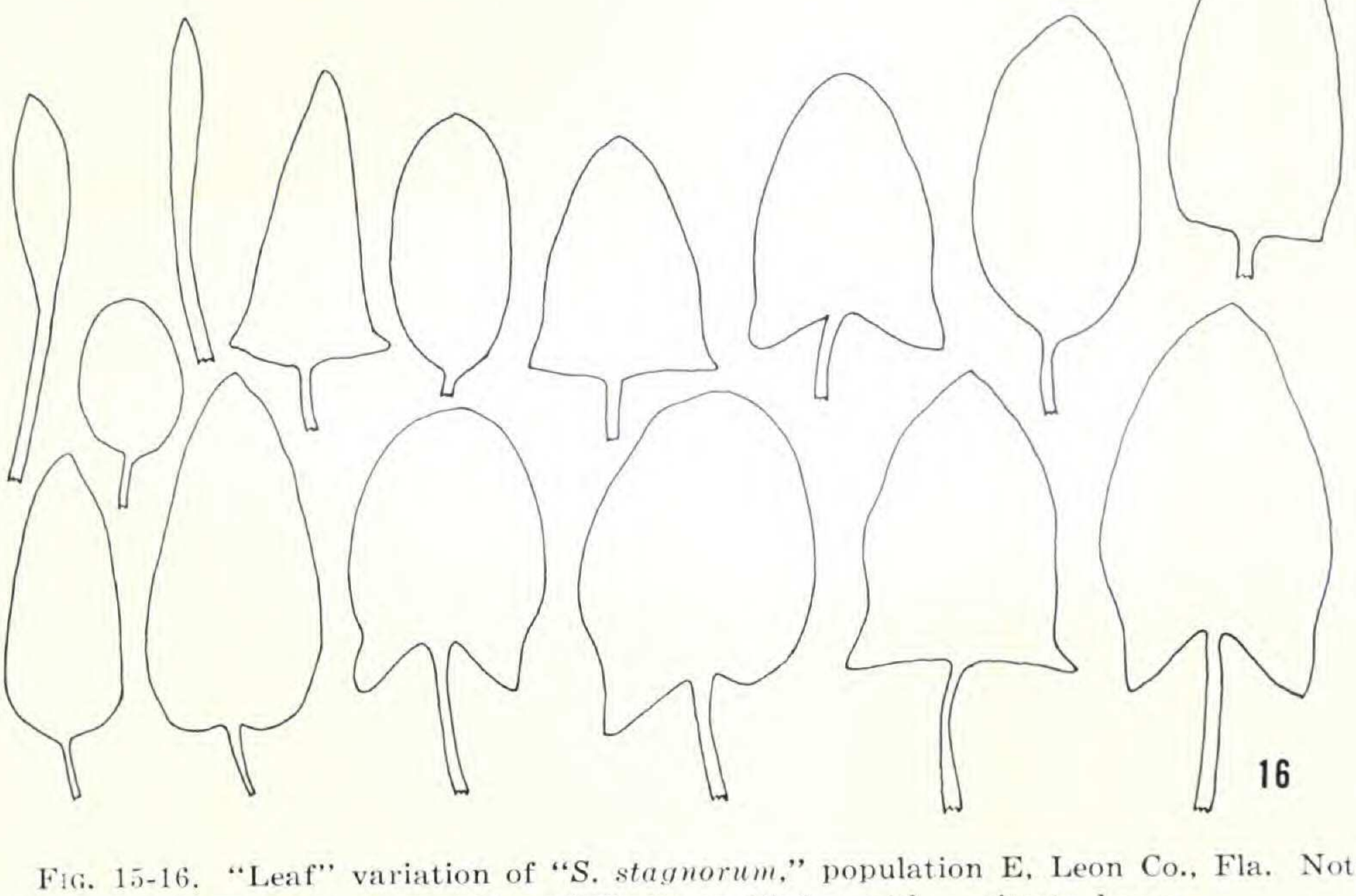


FIG. 15-16. "Leaf" variation of "*S. stagnorum*," population E, Leon Co., Fla. Note transition from narrow straplike phyllodia to blades with sagittate bases.

(Fig. 17 b-e) were found along with some ribbon-like phyllodia. With increase in water depth the phyllodia become much more elongate (Fig. 17 f-i) while the floating leaves virtually ceased to be produced (at about 1 meter deep). The length of the scapes varied directly with the water depth, also. Similar observations have been recorded by the authors at numerous other stations.

Population G: Wakulla Co., Fla.

In McBride's Slough, a medium-sized spring-fed stream flowing into the Wakulla River, a *Sagittaria* not unlike the "*S. kurziana*" phase is extremely abundant (*Adams and Mitchell 754*, April 21, 1961, FSU, 18 sheets). In the fairly swift current of the deeper portions of the stream these plants have elongate, ribbon-like phyllodia (Fig. 11a, b) and correspondingly long inflorescence scapes. However, in the shallower water near the banks many plants with much

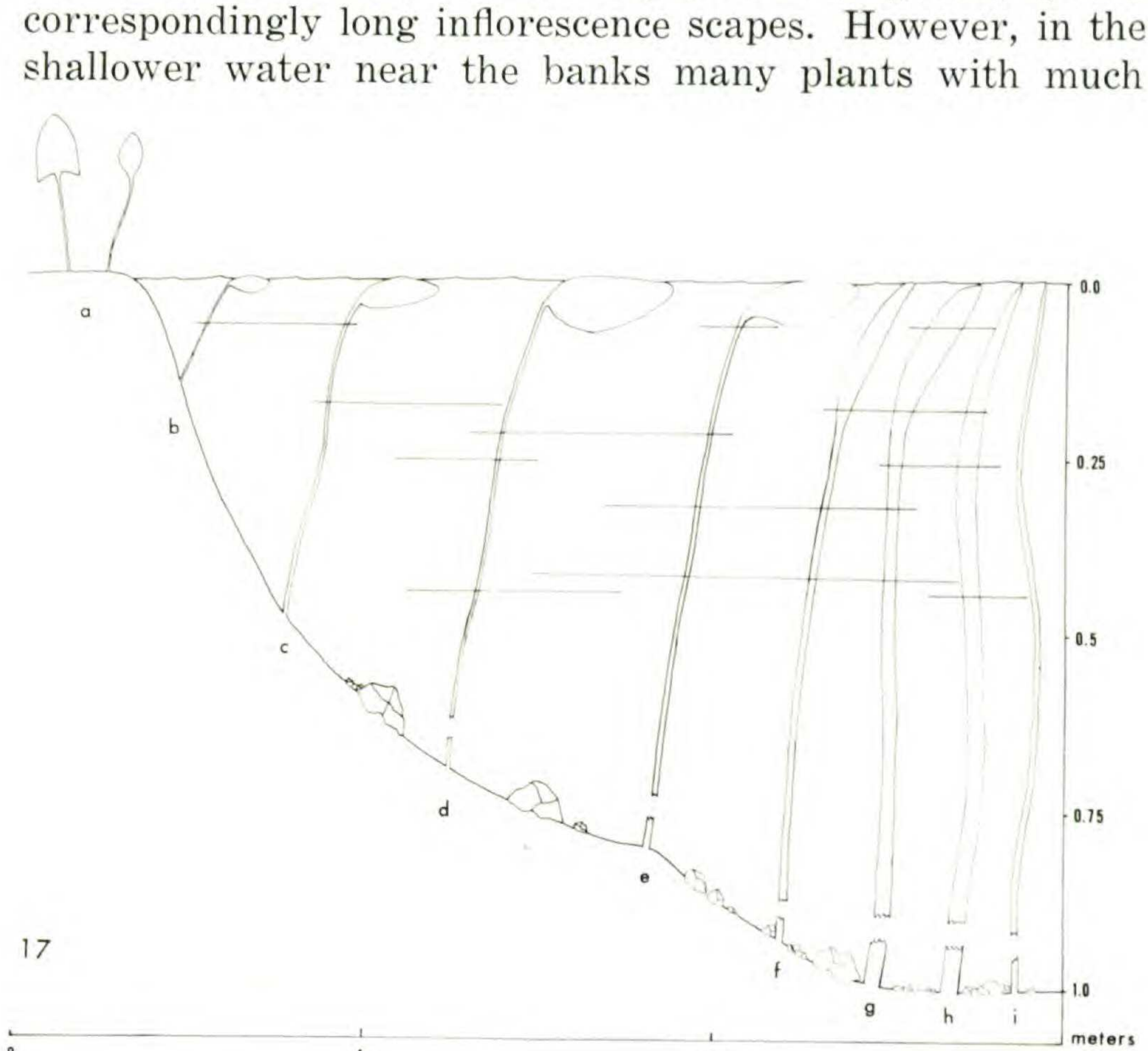


FIG. 17. Phyllode variation in "*Sagittaria stagnorum*." Diagrammatic representation of a transect from the shore out into the water of a drainage ditch. Water depth indicated by the ordinate. Transect distance by the abscissa. Phyllode length not to scale.

shortened phyllodia exhibiting various degrees of widening at the tips occur (Fig. 11 c-i). At the spring itself, the "*S. kurziana*" aspect is present in the deeper water but a gradual decrease in the size of the plants occurs toward the periphery of the springhead pool. On the soft mud at the edge of the pool, the leaves on individual plants show a gradual increase in dilation of the apex, not infrequently even producing a floating blade (Fig. 11 j-r).

Population H: Wakulla Co., Fla.

Approximately a mile north of the village of Newport is a sulfur spring which forms a small stream emptying into the St. Marks River. In the swift current of this rivulet there occurs a *Sagittaria* with elongate strap-like phyllodia hardly distinguishable (if at all) from the "*S. kurziana*" phase so abundant in the nearby river (see Fig. 1). Along the muddy banks and in quiet backwaters created by large masses of *Cicuta* (and other vegetation) plants whose phyllodia are variously dilated are frequently encountered. Occasionally some of these individuals produce phyllodia with widened, floating blades not unlike those characteristic of the "*S. stagnorum*" phase (Fig. 13). On the muddy banks along the lower portion of this stream (near its junction with the river) are plants which are very difficult to distinguish from the "*S. subulata*" form (similar to Figs. 4, 10 a-i) so very abundant further downriver where tidal fluctuation occurs (*Adams and Mitchell 755*, April 21, 1961, FSU).

Observation on Methods of Reproduction

Extensive vegetative reproduction via underground runners and corm-like structures is present in the *Sagittaria subulata* complex. The runners extend from the base of a plant and, after becoming several centimeters long, produce small white swellings similar to a corm or tuber (Figs. 1, 4, 12). From each such structure a new plantlet will arise. Not long afterwards, a new runner may form from the base of the young plant, a process often resulting in several to as many as fifty plants linked together (Wakulla Co., Fla., St. Marks River, 2 miles north of St. Marks, *Henderson 2021*, July 21, 1959, FSU, 3 sheets). Such a phenomenon is responsible for the formation of vast mats or beds containing

practically nothing but *Sagittaria*. In the Wakulla and St. Marks rivers large clumps of the "*S. subulata*" form often become detached from the tidal mud, float about on the surface, and are carried along by the current. Frequently the plants in these floating mats remain alive long enough to flower and produce mature fruits. Individual plants of the "*S. kurziana*" aspect are occasionally torn loose from their anchorage in the river bottom. If they happen to become caught-up in debris along the shore, or in quiet backwaters, very short phyllodia with dilated tips may be produced (Fig. 3). Flowers on greatly shortened inflorescence stalks are often formed, even remaining long enough to mature the achenes. Young plantlets may often form at the lowest node of the inflorescence. Several instances of this phenomenon have been seen on plants in McBride's Slough (*Adams 754A*, April 21, 1961, FSU).

Vegetative reproduction appears to be of paramount importance in the maintenance and local spread of plants of the *Sagittaria subulata* complex. The massive beds such as those formed in the Wakulla and St. Marks rivers replenish their numbers simply by the new plants which form from the corms produced on the subterranean runners. It would appear that, in these dense "carpets and meadows" of *Sagittaria*, seedlings would have little chance of becoming established, presumably being hindered by competition with existing plants which originated from the runners.

Reproduction by seeds no doubt occurs but probably plays a secondary role in the life cycle of these plants, at least once a colony becomes established. Re-establishment of the "*S. stagnorum*" phase following severe drouth resulting in drastic and often lengthy desiccation of the habitats is probably due to seeds. The junior author has observed situations where, after a severe drouth cycle of several years, no *Sagittaria* plants could be found in the dried-up ponds, ditches, and swamps. The drought was broken by much autumn rain following which these habitats rapidly became filled with water — and in the following very early spring the "*S. stagnorum*" form was found to be extremely abundant in the very same places were none was present earlier. This

observation implies that such rapid re-colonization may have been due to seeds since the underground runners would most likely have been killed by the several years of drouth. Abundant seeds are matured by the plants of the *S. subulata* complex.

The pedicels of the carpellate flowers become reflexed after pollination (Figs. 1, 3, 4, 12) and the fruits reach maturity underwater. The fruit, a distinctive achene with variously developed wings, becomes detached from the receptacle and floats to the water surface. We have not been able to follow the subsequent events leading to germination of the seeds.

Notes on Flowering

Plants of the "*Sagittaria kurziana*" phase flower throughout the year. The other phases of the *S. subulata* complex apparently cease flowering in the winter. Beginning in March and April in the Tallahassee region blooming resumes and continues until about November. In Massachusetts *S. subulata* var. *gracillima* (= *S. stagnorum* Small?, see below) begins to flower about the middle of June and continues until the end of July (note attached to C. E. Faxon's specimens in the Gray Herbarium).

Usually the pedicillated flowers are held a centimeter or two above the water surface during anthesis, the pollination appearing to be due to small flies. In the tidal flats where the "*Sagittaria subulata*" phase occurs the flowers open when the tide is low, thus permitting them to be pollinated. On the deep water side of the mud flats we have seen partially-opened flowers and these appear not ever to have become emersed. Although in all the phases the staminate flowers usually are emersed at anthesis, there is as yet considerable question as to whether many female flowers (which ultimately produce achenes) are ever emersed.

Observations on the Inflorescence Bracts

Each whorl of branches in the inflorescence of *Sagittaria* was described by Bogin (1955) as being "almost always subtended by a ring of 3 bracts." In the *S. subulata* complex these "bracts" were said to be "typically connate at the base, sheathing, . . . and occasionally spathe-like." Our observa-

tions on living plants show that these so-called bracts are actually the split and withering portions of a floral envelope which completely encloses the young inflorescence and flower buds. As these organs develop, the floral envelope is split down one side nearly to the base, producing a spathe-like appearance. Frequently, similar tears occur in the other sides, often producing a 3-parted "bract" structure like that illustrated by Bogin. Shortly afterwards, the envelope begins to wither and die, usually breaking away, leaving a narrow "ring" of chlorophyllous tissue at the node. The floral envelope may reach a length of 2-3 cm. in plants of the "*S. kurziana*" phase, especially at the lowermost whorl of the inflorescence. A similar envelope covers the corms, and is split by the growth of the young shoot.

Chromosome Counts

Several mitotic chromosome counts on plants identified as members of the *Sagittaria subulata* complex have been published. Brown (1946) reported the diploid number of 22 chromosomes for "*S. stagnorum* Small", "*S. Kurziana* Glück", and a putative hybrid between plants of these two taxa. A diploid count of 22 chromosomes in plants of the tidal "*S. subulata*" was published by Baldwin and Speese (1955). Brown (1946) also found 22 chromosomes in somatic tissue of plants which he identified as "var. gracillima." No mention of this report was made by Bogin (1955) who claimed to have discovered "ca. 44" chromosomes in root tips of "var. *gracillima*."

Remarks on the status of S. subulata var. gracillima

Since being described by Sereno Watson (1890), this *Sagittaria* with very narrow elongate phyllodia has been subjected to a variety of opinion concerning its biological distinctness and its taxonomic standing. Most authors have recognized its close affinity with the *S. subulata* complex but their interpretations of its alliance within the group have varied considerably. Watson considered the plant to be a variety of *S. natans* Michx. (*S. stagnorum* Small) while Smith (1895) treated it as a variety of *S. subulata* (L.) Buch. Many years later Fernald (1940) concurred with

Smith's opinion but the following year Clausen (1941) regarded var. *gracillima* as a deep water phase of the tidal flat plant *S. subulata*. Recently, Bogin (1955) and Beal (1960) have maintained *gracillima* as a variety of *S. subulata*.

Exception to the prevailing opinion concerning the relationship of var. *gracillima* was made by Pierce (in Gleason, 1952). This author concluded that the plant was more properly interpreted as a "deep water form" of *Sagittaria graminea* Michx.

Our observations of the *Sagittaria subulata* complex strongly suggest that var. *gracillima* may represent merely the deep water aspect of "*S. stagnorum*." We have seen many plants of the "*S. stagnorum*" phase in Florida and Georgia, both living and on herbarium sheets (Figs. 14d, 17i), which are hardly distinguishable from New England specimens (Fig. 6) traditionally classified as this variety. As discussed above, plants of "*S. stagnorum*" growing in water about a meter or more deep possess very elongate narrow phyllodia (Figs. 14 A, 17 i). The production of dilated leaf blades by plants of var. *gracillima* from Massachusetts similar to *House 25070* (Fig. 7) further suggests its close affinity with the "*S. stagnorum*" phase of the *S. subulata* complex.

Concluding Remarks

Despite the not inconsiderable amount of observation detailed in the foregoing discussion, we still do not feel justified in assigning taxonomic status to the three relatively distinguishable phases (Figs. 1, 4, 12, 13) in this complex. We believe that their biological discreteness, or lack of it, must be investigated more thoroughly, probably entailing the following: a more intensive and extensive analysis of populations or stands in relation to variable and fluctuating environments; reciprocal transplants; experimental culture; more exact and more extensive cytological study; and, if possible, crossing experiments. The universal occurrence of vegetative reproduction and the consequent impossibility of discerning individual plants in this complex certainly require that population analysis be handled differently from

that in groups whose populations are comprised of manifestly discrete individuals. Possibly plants can be grown satisfactorily from seed thus yielding information not otherwise available. — DEPARTMENT OF BOTANY AND BACTERIOLOGY, DEPAUW UNIVERSITY AND DEPARTMENT OF BIOLOGICAL SCIENCES, FLORIDA STATE UNIVERSITY.

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